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**WEST AMERICAN SPECIES OF THE
BIVALVED GASTROPOD GENUS *BERTHELINIA***

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INTRODUCTION

So synonymous are the terms "bivalves" and "pelecypods" in our minds that even the layman is disturbed by the phrase "bivalved gastropod," feeling it is somehow contradictory. The detection of these unorthodox snails by a Japanese zoologist, Dr. Siro Kawaguti, in 1959, was a dramatic moment in malacology. It was, however, the second of two noteworthy molluscan discoveries of recent years that have opened new windows toward the past and have modified the standard classification. The first and major find, of course, was *Neopilina*, a limpet-like mollusk showing segmentation of its soft parts, which was dredged in very deep water off the west Central American coast (Lemche, 1957). Although such mollusks did not seem as newsworthy in the popular press as, say, the coelacanth (a fish supposedly extinct since Jurassic time), *Neopilina* actually was more astonishing, for its ancestors left their last trace in the fossil record during mid-Paleozoic time. Recognition of a separate molluscan class, Monoplacophora, resulted.

The bivalved gastropods turn out also to be living fossils, though not of such antiquity. No new major category must be erected, but several genera hitherto assumed to belong in Pelecypoda now must be shifted to Gastropoda, so that in effect a new definition of the dividing line between these two molluscan classes is required.

The first report on the Japanese discovery appeared late in 1959; within the year since, a half-dozen papers on the subject have been published and more are in press. This literature has been summarized by Keen (1960b); a paper by Burn (1960b) appeared later.

The present report covers west American occurrences of the bivalved gastropods, with a review of species elsewhere and an attempt at classification of the group as a whole. Dr. Kawaguti has already investigated the soft parts of the Japanese form and the developmental stages of the animals. A cursory examination of soft parts of our material reveals no evident differences and so we will confine our study to the shell alone, leaving for interested zoologists a more detailed comparison of the two.

The bivalved gastropods are mostly small, the shells ordinarily less than 10 mm. in maximum length, the animal itself being not much longer in its extended position. These snails feed on green algae of the genus *Caulerpa*. Both the tissues of the animal and the shell itself take on the same shade of green as the alga, making detection of the living animals in place very difficult. The left valve bears a spiral nucleus, which is retained throughout life. Within, there is a conspicuous subcircular central muscle scar. A thin periostracum covers both valves, which peels off readily if the valves are left in water after the animal dies. At the dorsal junction or hinge of the two valves the periostracum thickens and forms a crude ligament that is set into vague notches. The second valve is not a modified operculum, as one might hastily assume. Dr. Kawaguti (1960), who has kept several generations of the animals in his laboratory, shows that the second valve appears between the third and seventh days of larval life as an area of calcification alongside the left margin of the aperture. Two separate lobes of shell material continue growth, held together by the periostracal layer.

More than one author has, in the past, described species and genera that we now see are related to the Japanese find. When single left valves were all that were known, the species were assigned to Gastropoda. Bivalvedness has been so taken for granted as the hallmark of Pelecypoda that no one has questioned the propriety of transferring these species and genera out of Gastropoda whenever matching valves came to light, although some comment would usually be made as to the remarkable resemblance of the shells to those of opisthobranchs. Without the evidence of soft parts, any other course would have been unthinkable. Thus, when the Japanese authors Kawaguti and Baba came to describe their find, they were not in a position to question the placement of such a group as *Edenttellina*, an Australian genus of supposed pelecypods, and they merely called attention to its superficial resemblance to the genus *Tamanovalva*, which they proposed as new. Their description sparked a fresh search for a living example of *Edenttellina*, which, when found, proved to be a gastropod, as did also a west American form. With this evidence, we can now infer that certain fossils with similar shell form,

supposedly pelecypods, classified hitherto in Galeommidae and Juliidae, actually belong in Opisthobranchiata, in a specialized division known as Sacoglossa, of which the genera *Oxynoe* and *Lobiger* have been the best-known representatives. Interestingly, all of these snails seem attracted to the green alga *Caulerpa*.

Reviewing these named groups and noting the general similarity of form among both the fossil and the Recent genera, one is tempted to regard them all as probable synonyms of the earliest, which would be *Berthelinia* Crosse, 1875. However, a closer study of the illustrations and of available material reveals that there are detectable, though slight, differences. How significant these are we cannot at present say, until more material can demonstrate whether the differences are merely points in one variable plexus or represent genuine divergences in the evolution of these snails. It has seemed best to us, therefore, to retain these named taxa — insofar as possible — as subgenera.

REVIEW OF THE CLASSIFICATION

Subclass OPISTHOBRANCHIA Milne-Edwards, 1848

Order SACOGLOSSA Von Ihering, 1876

Suborder TAMANOVALVIDA Kawaguti and Baba, 1959

(*ex* Tamanovalvacea Kawaguti and Baba, 1959)

Family JULIIDAE Dall, 1898

(= Prasinidae Stoliczka, 1871)

Small, bivalved, greenish shells, with a more or less well developed spiral nucleus in the left valve, posterior to the vertical mid-line; interior with a subcentral adductor muscle scar that may be partially or completely divided (*i. e.*, either circular or hour-glass-shaped).

Subfamily JULIINAE

Cordate shells with a heavy hinge having a prominent tooth-like ridge in one valve and a fossette-like fold in the other; apical nucleus present in young stages, obsolete in adult; adductor scar with a central constriction or even divided into two parts, one above the other.

The type genus, *Julia* Gould, 1862 (synonym, *Prasina* Deshayes, 1863), is widely distributed in the Pacific. Its type species is *J. exquisita* Gould, from Hawaii. Although several species of *Julia* have been reported — from Madagascar to Japan and the west coast of Central and South America, as well as from fossil strata of Oligocene and Miocene age in Europe and the Caribbean — little is known about habits and ecology. The assignment to Gastropoda is on the basis of the analogy of the shell to that of other known bivalved gastropods.

Subfamily BERTHELINIINAE Beets, 1949

Shells lenticular in shape, ovate to quadrate, with a weak hinge; spiral nucleus in one valve retained in the adult; adductor muscle scar central, undivided, circular.

Genus *Berthelinia* Crosse, 1875.

Berthelinia CROSSE, 1875, Jour. Conchyl., vol. 23, p. 79

TYPE SPECIES. *B. elegans* Crosse, 1875, by monotypy. Middle Eocene, Paris Basin, France.

DIAGNOSIS. Left valve with spiral nucleus; right valve slightly smaller, without spiral apex; outline of shell somewhat quadrate. Color of shell, in living forms, greenish to yellowish.

REMARKS. The type specimens of *B. elegans* are in the collection of the *Journal de Conchyliologie*, Paris. Dr. Edouard Fischer reports (letter dated 15 October 1960) that of the original five specimens catalogued in 1898 only two are extant, the larger measuring 1.5 mm. in length. Three other specimens have been available to us for study, in the Cloez collection, Museum of Paleontology, University of California, Berkeley. These, like the specimens examined by Dr. Fischer, match well the original illustration in the *Journal de Conchyliologie* (vol. 23, pl. 2) and those by Cossmann reproduced here (figs. 7, 8).

Subgenus *Berthelinia*, s.s.

DIAGNOSIS. Posterior end of shell somewhat set off by a ventral sinus. Size, minute (2 to 3 mm.). Hinge plate in left valve widened at ends, without teeth but with faint corrugations.

ADDITIONAL SPECIES.

B. elegans elata Cossmann, 1888. Upper Eocene, France.

B. schlumbergeri Dautzenberg, 1895. Recent, Nossi-Bé, Madagascar

B. elongata Cossmann, 1906. Eocene, France.

The last two species are referred to *Berthelinia* s.s. with some reservation, as we have not seen specimens.

Subgenus *Ludovicia* Cossmann, 1888, ex Deshayes MS.

Ludovicia COSSMANN, 1888. Ann. Soc. r. Malac. Belgique, vol. 22 (for 1887), page 45.

TYPE SPECIES. *L. squamula* Cossmann, 1888, by monotypy. Middle Eocene, France. (Word has just been received from Professor Edouard Fischer that the holotype of *L. squamula* cannot be located and is presumed lost.)

DIAGNOSIS. Hinge weak to edentulous, with posterior dorsal margin widened and somewhat reflected; outline of shell inequilateral, rounded-trigonal to oblique; size of shell, large for the genus (to 15 mm.).

REMARKS. Type material of *Ludovicica* was not available for this study, but a single left valve in the Cloez collection, Museum of Paleontology, University of California, furnished valuable information. This specimen measures 6.5 mm. in length, less than half the size cited by Cossmann. The tip of the nucleus is broken off. The hinge is narrow but shows a slight prominence along the margin that might be interpreted as an incipient tooth. The central muscle scar, not shown by Cossmann, is apparent (figs. 25,26). Otherwise, the shell matches Cossmann's illustration well (figs. 3,4).

Subgenus *Anomalomya* Cossmann, 1888.

Anomalomya COSSMANN, 1888, Ann. Soc. r. Malac. Belgique, vol. 22 (for 1887), p. 169.

TYPE SPECIES. *A. corrugata* Cossmann, 1888, by monotypy. Upper Eocene, France.

DIAGNOSIS. Hinge with a fossette at posterior end in right valve, a tooth in left. Outline somewhat rounded. Size moderate (5 to 6 mm.).

ADDITIONAL SPECIES. An unnamed form (*vide* Burn, 1960b, p. 45) in South Australia, figured by Hedley (1920, figs. 1-5) as *Edenttellina typica* (figs. 11-15), would seem to belong here (see figs. 9, 10 for a reproduction of Cossmann's original figure of *A. corrugata*).

Subgenus *Edenttellina* Gatliff and Gabriel, 1911.

Edenttellina GATLIFF and GABRIEL, 1911, Proc. R. Soc. Victoria (n.s.), vol. 24, page 190.

Tamanovalva KAWAGUTI and BABA, 1959, Biol. Jour. Okayama Univ., vol. 5, pts. 3-4, p. 178 (type species, by monotypy, *T. limax*, Recent, Japan).

TYPE SPECIES. *E. typica* Gatliff and Gabriel, by monotypy. Recent, Victoria, Australia.

DIAGNOSIS. Hinge as in *Bertbelinia*, strict sense, but with the hinge plate more nearly uniform in width, the outline of the shell more rounded, tending to be trigonal in adult with at most only a slight ventral sinuosity. Size, moderate (to 9.5 mm.).

ADDITIONAL SPECIES:

Scintilla? *chloris* Dall, 1918. Magdalena Bay, Baja California.

Edenttellina corallensis Hedley, 1920. Queensland, Australia.

Tamanovalva limax Kawaguti and Baba, 1959. Japan.

Bertbelinia (*E.*) *chloris belvederica* Keen and Smith, new subspecies, La Paz, Gulf of California.

REMARKS. Conchologically, the shells of *Tamanovalva* seem inseparable from those of *Edenttellina*. It is possible that anatomical differences may be found that will justify retention of *Tamanovalva* as a subgenus. As Burn has reported (1960b, p. 46), Dr. Baba has observed a distinction in the formation of the apices in the radular teeth, which may or may not prove to be significant when more material becomes available for study.

Genus *Midorigai* Burn, 1960.

Midorigai BURN, 1960, *Nature*, vol. 187, no. 4731, pp. 45-46. figs. 8-14.

TYPE SPECIES. *M. australis* Burn, by original designation. Recent, Victoria, Australia.

DIAGNOSIS. Outline nearly rectangular; spiral nucleus of left valve not erect but reflected backward over hinge margin; adductor scar composite, with a flange that rises to a smaller scar under the hinge.

REMARKS. The inclined and flattened nucleus is so distinctive that this group may prove worthy of generic separation, as its author proposed. However, the muscle scar pattern (which unfortunately was not illustrated) seems to be at least simulated in some specimens of *Berthelinia chloris belvederica*, in which a faint line can be traced from the end of the central scar up to a smaller one under the margin of the hinge.

WEST AMERICAN BERTHELINIINAE

Berthelinia (*Edenttellina*) *chloris chloris* (Dall), Text figure 20.

?*Scintilla chloris* Dall, 1918. *Proc. Biol. Soc. Washington*, vol. 31, p. 5.

Scintilla (?) *chloris* Dall. Keen, 1958, *Sea Shells of Tropical West America*, p. 108, fig. 235. (Figure of presumed type specimen).

TYPE LOCALITY. Magdalena Bay, Baja California, C. R. Orcutt, collector.

REPOSITORY. U.S. National Museum, No. 218179.

ORIGINAL DESCRIPTION. "Shell of a pale green color, translucent, with more or less evident paler rays, the umbo darker than the rest of the disk; inequilateral, rather compressed, the posterior end wider, longer, rounded; the anterior end shorter, attenuated; the exterior polished, with slight concentric irregularities of growth, and extremely faint, partly obsolete radial striulae; hinge with a long amphidetic ligament in front of which in the left valve is a single noduliform denticle, and behind which is a feebly indicated lateral lamella; the scar of the ligament is long and narrow, there is no evident division into ligament and resilium which might perhaps be visible in a perfectly fresh specimen. The interior of the disk is so polished that the muscular and pallial scars are not distinguishable, but under the microscope a sparse punctation can be made out; the margins are entire. Length of

valve, 9.0; length of the part in front of the vertical from the umbo, 3.0; height, 6.0; double diameter of the left valve, 2.0 mm. . . Two left valves were obtained. . . ."

REMARKS. The discrepancy between Dall's mention of two left valves and the obviously opposite valves in the photograph of the presumed type at the U.S. National Museum—sent upon request for publication in 1958—came to light with the intensive study of newly collected material in Baja California. Dr. W.P. Woodring kindly made a restudy of the type lot and reported (letter to A.M. Keen dated February 16, 1960) that the two matching valves (apparently a pair but with the "right" one [upper figure in Keen, fig. 235] chipped along the ventral edge) are now labelled "Type," No. 218179, but were entered in 1918 merely as "*Scintilla*" and as "½ specimen," or one valve. A smaller "left" valve now labelled "Paratype," No. 610355, was entered in 1958 as "*ex* 218179." The three shells are practically transparent, and the only color seems to be from a thin and irregular coat of shellac, applied for preservation. Dimensions as taken from the photographs would be: "right" valve, length, 8.8, height 5.8 mm.; "left" valve, length, 8.4, height, 5.6 mm. These dimensions, though differing from Dall's statement, are proportional to his 9.0/6.0. The problem raised by the additional valve perhaps is resolved by a specimen now at the California Academy of Sciences (fig. 20) from the Orcutt Collection. It is from Magdalena Bay and carries an original label in Dall's handwriting: "*Scintilla*, n. sp." We interpret this as being one of the two original "left" (actually, right) valves, a conclusion strengthened by the fact that this specimen exhibits the paler rays mentioned by Dall. This and the "½ specimen" of U.S.N.M. No. 218179 would constitute the original lot. Perhaps by the time Orcutt received back his submitted specimen, he had sorted out more valves and then forwarded them to the National Museum to supplement the single valve remaining there. Dimensions of the California Academy syntype are: length, 9.4 mm., height, 6.5 mm., diameter (one valve), 1.8 mm. Dall's stated dimensions seem to be the average for the two syntype "left" valves, but his "double diameter" of 2.0 mm. is at variance both with the California Academy specimen and with the evident degree of inflation shown in the photograph. Ratios used elsewhere in this paper are therefore computed from the measurements of the available California Academy specimen. The subcentral adductor muscle scar shows clearly when one knows where to look for it. The habitat of *B. chloris chloris* is not known, as Orcutt's material was obviously from beach drift.

Berthelinia (*Edentellina*) *chloris belvederica* Keen and Smith, new subspecies.
(Figures 18, 19, 21-24, 27-32. Plate 5, lower figure.)

HOLOTYPE. No. 12317, Paleo. Type Coll., California Academy of Sciences.

PARATYPES. Paleo. Type Coll., CAS Nos. 12318, 12318a-c; No. 9172, Stanford Univ. Paleo. Type Coll. Other specimens in collections of California Academy of Sciences; U.S. National Museum; British Museum (Natural History); University of California Museum of Paleontology; National Museum of Victoria, Australia; Universities of Osaka and Okayama, Japan; Instituto de Biología, Mexico; Museum d'Histoire Naturelle de France; Museum of Comparative Zoology, Harvard; Academy of Natural Sciences, Philadelphia; National Museum of Canada; Zoologisk Museum, Copenhagen; Naturhistoriska Riksmuseet, Stockholm; and others.

TYPE LOCALITY. Puerto Ballandra Bay, about 10 miles northeast of La Paz, Baja California. Allyn G. Smith, collector, 4 October, 1960.

ADDITIONAL LOCALITIES. Espíritu Santo Island, on northern margin of Candelero Bay, about $\frac{1}{2}$ mile south of Isla Partida, Myra Keen and Allyn G. Smith, collectors, 31 August, 1960; Puerto Ballena, Espíritu Santo Island, Myra Keen and María Luisa Valdez de Adcock, collectors, 19 December 1960.

DIMENSIONS. Holotype (largest specimen): Length, 8.5 mm.; height, 5.5 mm., convexity or diameter (both valves), 2.5 mm. Comparable measurements of an average-sized specimen: length, 5.8 mm., height, 3.9 mm., convexity (both valves), 1.6 mm. Ratio of diameter to height, 0.33 to 0.47, average 0.41.

DESCRIPTION. Shell small, thin, translucent green in color, with a whitish-iridescent sheen internally; periostracum nearly transparent, most evident along hinge margin, where it becomes thickened into a weak ligament; outline ovate-trigonal in adult, trapezoidal in young shells, the anterior end broadly rounded, the posterior more pointed, a slight radial angulation marking off a posterior slope in some specimens; sculpture of growth lines and a few faint radial striae; nucleus on left valve only, whitish, of $1\frac{1}{4}$ turns, sharply set off from the rest of the shell by a change in color and texture; adductor muscle scar relatively large; hinge weak, with a small amount of ligamental material and faint pitting of the shell rim.

COMPARISONS. Specimens of *B. (E.) limax* (Kawaguti and Baba) have been available for study, both as live animals and as preserved material (Smith, 1960a) through the courtesy of both authors. The most evident differences between the two species are in the smaller nucleus of *B. limax*, which has only a single turn, and the slightly greater inflation of the valves. Sample dimensions: length, 5.8 mm., height, 3.7 mm., diameter (both valves), 1.7; ratio of diameter to height, 0.46.

Judging from the illustrations of *B. typica* (Gatliff and Gabriel) recently published by Burn (1960b, figs. 1-7), that shell is more trigonal than in *B. c. belvederica*, with a more pointed posterior end and a nucleus that may be more conspicuous. Burn regards *B. corallensis* (Hedley) as a synonym of *B. typica*. He also points out that the figures by Hedley (which have formed the concept of *B. typica* for most malacologists) actually are of an unnamed

form from South Australia. We suggest that it may belong in the subgenus *Anomalomya*.

The three specimens of *B. elegans* examined for this study as well as the original figures show a more trapezoidal outline than in *B. c. belvederica*, with more definite hinge structures, the hinge margin slightly pitted or denticulate; also, the shells are smaller, less than 3 mm. in length.

The identification of the present form simply as *B. chloris* (Dall) would seem logical, and in fact this was our determination for the first valve, taken in beach drift on Espíritu Santo Island in November, 1959. It was thought to be a young specimen and to constitute an extension of range from Magdalena Bay, on the outer coast of Baja California. However, statistical comparison of the available syntype with a growth series of the La Paz material convinces us that they are significantly different. The largest shell of typical *B. chloris* is a full millimeter longer than the longest one of *B. c. belvederica*. This might not be a constant difference, but the difference in convexity is, for the valves of *B. c. belvederica* are flatter at every stage of growth. The height-diameter ratio for *B. chloris chloris* is 0.55, as compared to 0.46 for *B. limax* and 0.33 to 0.47 (average 0.41) for *B. c. belvederica*. Also, the hinge of the *B. c. chloris* is markedly wider and stronger, with a prominent lamellar tooth at the posterior end. Figures 18 and 19, drawn to the same scale, show the contrast. It would seem, then, that there are two forms of *Berthelinia* in Baja California, the one on the inner coast, the other on the outer.

HABITAT. Living specimens of *Berthelinia* were first taken in the La Paz area on 30 August, 1960, at an 8-foot depth close to shore among large blocks of volcanic agglomerate broken from an adjacent rock wall at the north edge of Candelero Bay, Espíritu Santo Island, one-half mile south of Isla Partida. A small, loose clump of a feathery type of green alga (*Caulerpa sertularioides* [Gmelin] Howe) was brought up from the bottom by Sra. María Luisa Valdez de Adcock, which on careful search produced several small specimens. This type of alga being more prevalent in the sand and on dead coral chunks of the bay floor, about 100 yards to the south, further effort was concentrated there. Masses of the alga *Caulerpa* were brought up from depths of 5 to 8 feet. More living specimens were noted, as also a few living sacoglossan opisthobranchs of the genus *Oxynoe* (probably a new species). Water temperature was 82–84° F., air temperature about the same.

Some of the living specimens of *Berthelinia* were placed in a gallon-sized thermos jug, with an ample supply of the alga, for transportation to San Francisco by plane the following day. The remainder of the algae collected was transferred to plastic sacks, for more careful sorting. Unfortunately, the living specimens of *Berthelinia* and *Oxynoe* did not survive, for the *Caulerpa* was thickly inhabited by small sea anemones that, dying, fouled the water. The number of berthelinias later recovered amounted to around 35.

Quantities of minute mollusks also were found in the debris and some nudibranch egg masses, all of which were preserved for future study.

Another opportunity to try for living specimens of *Berthelinia* came on 4 October, 1960. At this time a search was made in Puerto Ballandra Bay, on the mainland of the peninsula north of La Paz. The sand of this bay did not have the masses of the feathery type of *Caulerpa*, although small patches of it were growing on the volcanic rocks in shallow water near the north end of the sand beach. This form of *Caulerpa* was clean of the troublesome small anemone. Careful search produced no specimens of *Berthelinia*. In the same general area, small patches of a second species of *Caulerpa*, *C. racemosa* (Forsk.) var. *turbinata* (J. Agardh) Eubank, occurred growing along the sides of and between the boulders. This was a "bunch-of-grapes" type, similar in its dark blue-green color and general characters to the Japanese *Caulerpa okamurai* brought by Dr. Kawaguti, differing only in that many of the terminal branches have a flat, disk-like end. *Berthelinias* were discovered on this alga in some quantity, ranging in size from juveniles to one adult with a shell length of 8.5 mm., which was selected as our type specimen. Water temperature at this location was 82–83° F., air temperature 84° F. Except for the warmer water, conditions here were precisely those described by Kawaguti in Japan and by Burn in Victoria, Australia. A fair-sized sample of the alga from Puerto Ballandra Bay was brought back to San Francisco for further scrutiny, and from it a total of more than 100 specimens was obtained, with more of *Oxynoe* and several specimens of a grayish nudibranch about an inch long.

EXPLANATION OF FIGURES

Figs. 1, 2, 5, 6. *Berthelinia elegans elata* Cossmann. Le Ruel, Upper Eocene, France. $\times 10$. (After Cossmann, 1888, pl. 7, figs. 24-27). Page 50.

Figs. 3, 4. *Ludovicia squamula* Cossmann. Parnes, Middle Eocene, France. $\times 1\frac{1}{2}$. (After Cossmann, 1888, pl. 2, figs. 21-22). Page 50.

Figs. 7, 8. *Berthelinia elegans* Crosse. Holotype, Courtagnon, Upper Eocene, France. $\times 10$. (After Cossmann, 1888, pl. 7, figs. 28-29). Page 50.

Figs. 9, 10. *Anomalomya corrugata* Cossmann. Le Fayel, Upper Eocene, France. $\times 4$. (After Cossmann, 1888, pl. 7, figs. 31, 30). Page 51.

Figs. 11-15. *Berthelinia (Anomalomya)* sp. Recent, South Australia. Length, 5 mm. (After Hedley, 1920, figs. 1-5). Page 51.

Figs. 16, 17. *Berthelinia (Edentellina) corallensis* (Hedley). Recent, Queensland, Australia [= *B. (E.) typica* (Gatliff & Gabriel), *fide* Burn, 1960] $\times 10$. (After Hedley, 1920, figs. 7-8). Page 51.

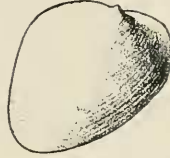
Figs. 18, 19. *Berthelinia chloris belvederica* Keen & Smith, new subspecies. Enlarged drawings of living animals in the active stage from color slides taken in the field. Page 53.



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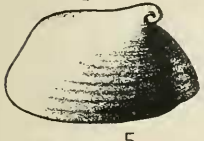
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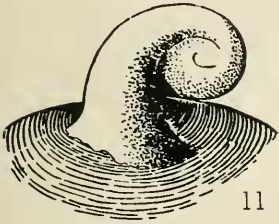
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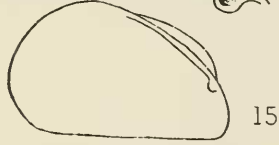
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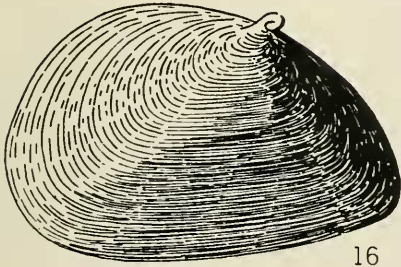
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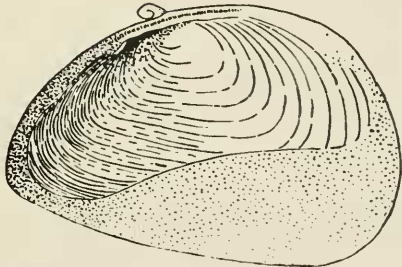
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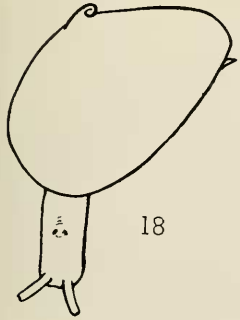
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Living specimens of *Berthelinia* and *Oxynoe* were photographed on board a boat at the site of collection, using an Exakta camera with extension tubes and electronic flash. Photography under improvised conditions proved difficult, mainly because the animals were so active, crawling over each other and either getting out of focus or spoiling the composition of the picture.

A second attempt was made to bring back specimens of both genera alive for laboratory observation, again unsuccessfully. Perhaps too much of the *Caulerpa* was put into the thermos jar in relation to the quantity of water.

On 18 December, 1960, six additional specimens were found on *Caulerpa racemosa* in Candelero Bay. These algae occurred sparingly in surge channels on the seaward side of a rock reef exposed at moderately low tide. The specimens ranged in size from 2.8 to 8.5 mm. in length. The next day four more were taken in Puerto Ballena, about a mile south of Candelero Bay, again on *C. racemosa*, which here grew in the closest possible association with the more abundant *C. sertularioides*, being intercalated among it on small rocks at the outer edge of a flat, shallow bay. Later, three more specimens of *Berthelinia* were picked out of dried samples of another green alga, *Halimeda* sp., that had been taken in slightly deeper water near the entrance to Puerto Ballena. Scrutiny of the live *Halimeda* material failed to reveal any mollusks

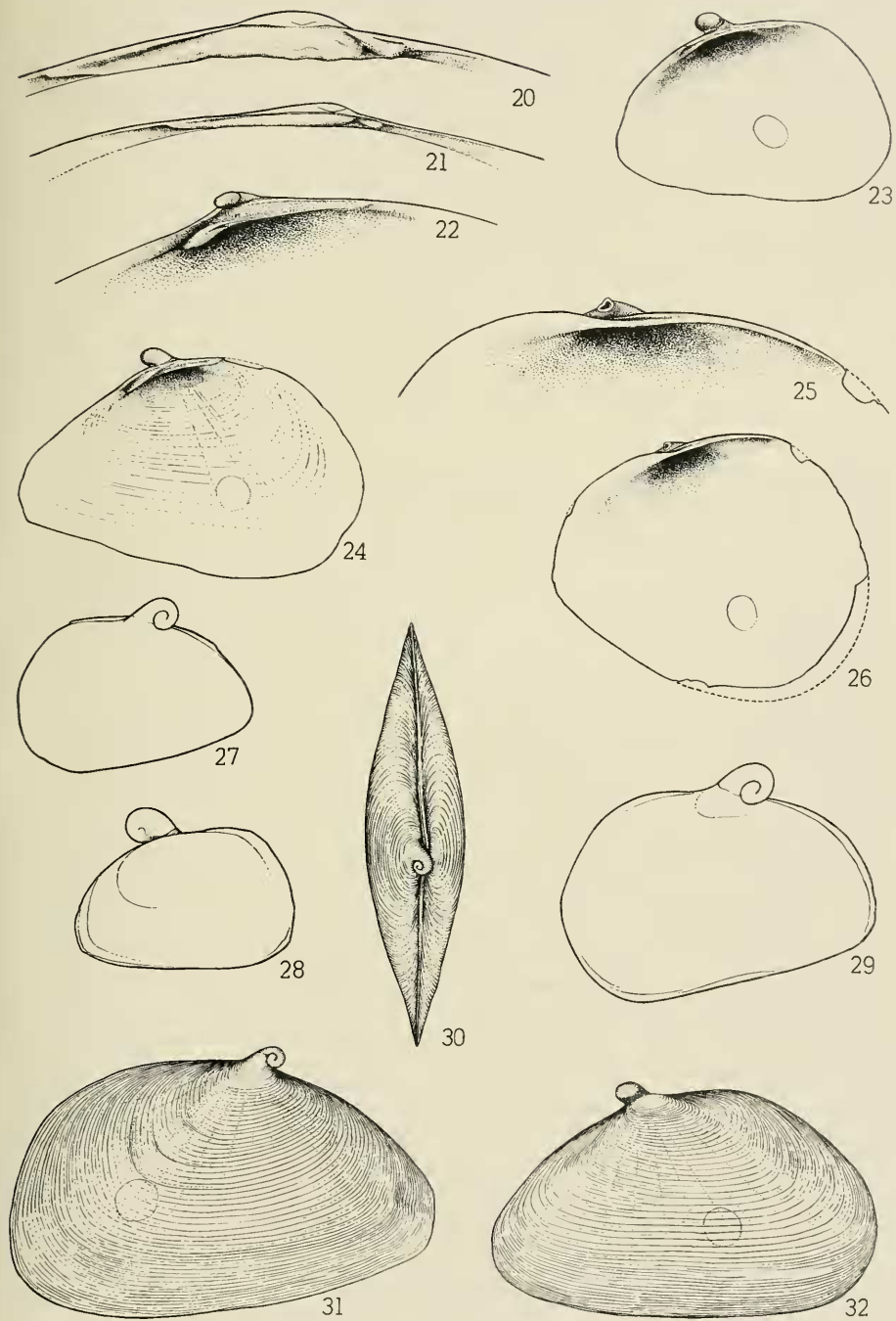
EXPLANATION OF FIGURES

Fig. 20. *Berthelinia (Edentellina) chloris chloris* (Dall). Syntype, CAS Paleo. Type Coll. No. 12316. Hinge of right valve. Recent, Magdalena Bay, Baja California. $\times 12.5$. Page 52.

Figs. 21, 22. *Berthelinia (Edentellina) chloris belvederica* Keen & Smith, new subspecies. Holotype, CAS Paleo Type Coll. No. 12317. Fig. 21, hinge of right valve; fig. 22, hinge of left valve. Recent, Puerto Ballandra Bay, near La Paz, Baja California. $\times 12.5$. Page 53.

Figs. 23, 24, 27-32. *B. (E.) chloris belvederica* Keen & Smith, new subspecies. Hypotypes, Stanford University Paleo. Type Coll. Nos. 9173a-e. Recent, Candelero Bay, Espiritu Santo Island, Baja California. Fig. 23-24, interior of young left valves, showing variation in hinge development; $\times 24$. Figs. 27, 29, exterior of left valve at two stages of growth of young shell, showing variations in outline but constant size of nucleus; $\times 32$. Fig. 28, exterior of right valve and reverse of nucleus of left valve; $\times 30$. Figs. 30-32, left and right dorsal views of a small, presumably adult specimen; length, 3.7 mm.; $\times 16$. Page 53.

Figs. 25, 26. *Ludovicica squamula* Cossmann. Hypotype, Museum of Paleontology, University of California (Berkeley). Neauphle, Middle Eocene, France. Fig. 25, detail of hinge; $\times 12.5$. Fig. 26, interior of left valve; $\times 6$. Page 50.



at all on the surface of the fronds. Possibly the berthelinias had been detached from nearby clumps of *Caulerpa* when the *Halimeda* was uprooted and carried ashore, but further field observations should be made at this place to determine whether *Berthelinia* can live also on *Halimeda*, as it can on the two species of *Caulerpa*. Also, further investigations should be made as to the preference of *Berthelinia* for the two species of *Caulerpa* where both occur in proximity, to ascertain whether individuals that live on the *C. sertularioides* are always smaller (the maximum size of those taken at Candeler Bay did not exceed 4 mm.) and whether they can transfer from the one alga to the other without ill effect.

On the third attempt, live specimens of *Berthelinia* were transported by air to California, in spite of poor temperature control. The specimens taken on 18 and 19 December, in water with a surface temperature of 72° F., had been kept alive in a field laboratory by floating them in vials, with bits of *Caulerpa* (which they refused to touch) placed in shallow pans of seawater. At the time of departure from the field, 21 December, a few clumps of the alga (especially one that was collected without damaging the holdfasts, for it grew on a small clam valve) were transferred to a gallon-sized thermos container, which was half filled with clean seawater. The specimens of *Berthelinia*, after a change of seawater, were dropped, still in their closed vials, into the thermos. The lid was left off the thermos for better aeration except when in actual transit on the boat and airplane, and the specimens survived, even through one night of the cool temperatures of the San Francisco Bay area. As soon as daylight was available, the *Caulerpa* clumps were removed to a shallow bowl, near a window, and covered with seawater that had been vigorously shaken. The berthelinias were then transferred to the bowl. They appeared to be dead, the bodies being relaxed and protruding from the shell, but some soon proved able to retract upon stimulation. Most of them failed to revive beyond this, gradually losing color as they died. Two, however, began moving about, carrying the shell valves partially open over the dorsal part of the body. On 24 December one was observed in the act of feeding on the tip of a *Caulerpa* frond and was photographed. Perhaps the alga, which no longer showed the bright and healthy green of fresh material, failed to provide sufficient nourishment, for by the next day this specimen was visibly weaker. It still could cling to the alga by a mucous thread. On 26 December — one week from the time of collection — it was obviously dead, losing the green coloration. Temperature tolerance for the species thus proves to be substantially as great as that of the Japanese form, in spite of a more tropical habitat.

ASSOCIATED FAUNA.

The green alga *Caulerpa* offers a microhabitat in which a number of invertebrates abound, notably the small anemone mentioned above and a small crab. There are also several species of mollusks occurring here in quantity that show up in beach drift only sparingly if at all. For

example, no specimens of *Amphithalamus stephensae* Bartsch were found in over a quart of drift from Candelerio Bay (in which the single first-seen valve of *Berthelinia belvederica* came to light), yet on the roots of the algae these were present by the hundreds. Almost as common at this place was *Tricolia cyclostoma* (Carpenter, 1864). It was also common at Puerto Ballandra Bay, but there the *Amphithalamus* was absent, at least in the sample taken. *Oxynoe*, n. sp., was fairly common at both places, as also *Jeffreysia bifasciata* Carpenter, 1864, and a small eulimid. About a dozen specimens of an undescribed columbellid resembling *Mitrella lalage* Pilsbry and Lowe occurred at Puerto Ballandra Bay. Further observations are needed to show what the relationship of all these mollusks is to the alga, whether feeding on it, as *Berthelinia*, or seeking protection beneath or among it.

THE SIGNIFICANCE OF BERTHELINIA

Berthelinia is noteworthy on two counts — for its unusual distribution and for its anomalous shell. Hitherto only one species has been reported in the eastern Pacific (Keen, 1960a, 1960b). Now a second form is added. Thus, the range of the genus in the Recent fauna extends from Madagascar and Japan south to southern Australia and across the Pacific eastward to inside the tip of Lower California. Within the quadrangle so encompassed lies the East Indies and the whole of Polynesia. Perhaps an intensive search there on *Caulerpa* would produce more records. In any case, so wide a distribution of a genus in the Recent fauna without intermediate representatives is puzzling until one examines the fossil record. During early Tertiary time there was a great sea, the Tethys, that stretched east and west across what is now Europe and southern Asia. Its fauna seems to have originated mainly in the warm, shallow waters of what is now central France and to have spread eastward as far as Japan and Australia and westward across the Atlantic into the Caribbean and even farther, through an open Panamic portal to the west coast of the Americas. The present-day areas of distribution of *Berthelinia* are, then, peripheral to the ancient Tethyan sea and mark almost the farthest advances of its fauna. Other genera might be cited (for example, *Nemocardium*, in the broad sense, or *Typhis*) that have a somewhat similar range in time and space, but few could be found with so wide a gap between known occurrences of species. The range in time from Eocene to Recent is somewhat bridged by the related genus *Julia*, which seems to have originated also in Europe during the late Oligocene, to have spread west to the Caribbean and east to the East Indies in Miocene time, and also to have survived peripherally in the Pacific and Indian oceans, being known today from Madagascar eastward to Japan, Hawaii, and the west coast of Central and South America.

The anomalous shell of *Berthelinia* raises the question of how we shall interpret the phenomenon of bivalvedness in Gastropoda. Is it analogous to

the first appearance of Pelecypoda, and does it imply that Pelecypoda branched out from Gastropoda in some such fashion? To answer this, one must look at the fossil record, which seems to indicate a negative reply to both questions. At the time the pelecypods first appeared, in late Cambrian or early Silurian time, the only gastropods present were rather simple limpet-like forms and notched-sided shells of the Pleurotomariidae, both not very far removed from Monoplacophora. Dr. C.M. Yonge and others have suggested that the pelecypod valves represent two areas of calcification that developed from either side of the body, bridged by tough chitinous periostracum of the outer shell layer, which in time became a hinge. The manner of outgrowth of the second valve in the juvenile *Berthelinia* lends force to this hypothesis. The *Berthelinia* group can, therefore, give us some insight into the mechanism of hinge formation, but we must not forget that the production of two valves is taking place in a gastropod family far removed from any family that could originally have given rise to Pelecypoda, so that this is no recapitulation of the original event, even granting a direct derivation of Pelecypoda from Gastropoda. It is interesting to note that the earliest pelecypods and the shelled sacoglossans have shells that are nearly smooth, not strongly ribbed. A development of a mortise-and-tenon joint — in other words, hinge-teeth and sockets — seems to be necessary for effective closure of the valves. Although in *Berthelinia* the teeth are neither consistent in size nor regular in shape and certainly not differentiated into cardinal and lateral areas as in clams, the very fact of their presence shows that the proper opening and closing of the two valves is facilitated by compensatory roughenings of the hinge surface. Why this two-valved device should have been adopted in Opisthobranchiata is a question we shall not try to answer here, though we may point out that this is a group of gastropods in which there has apparently been much evolutionary experimentation, even to the point of complete suppression of the shell.

The marked similarity in form of Eocene and Recent *Berthelinia* — so marked that we can separate them subgenerically only on rather minute points of difference — shows that during the last sixty million years or so, little or no evolutionary progress in the group has taken place. The mutation of bivalvedness occurred. It proved to be, if not advantageous, at least not unsuccessful. It persisted, but it evidently did not lead to organic change. We must suppose that the little Eocene snail wearing its two-valved shell looked much like its living descendant. The pelecypods, on the other hand, once they had achieved their tightly-closing double shell in that long-ago Paleozoic time went on to develop profound bodily changes, such as loss of the central or head ganglia and development of large, symmetrical gills, as well as to a change in habits, becoming sedentary or only clumsily mobile.

Hence it would seem that the principal significance of *Berthelinia* and the other Juliidae is that they demonstrate anew the dynamic pliability of what Yonge calls the mantle-shell, which can produce a bivalved structure

with an effective ligament and mortised tooth-and-socket junction from two quite unrelated stocks.

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PLATE 5

- (Upper figure) *Berthelinia (Edenttellina) limax* (Kawaguti & Baba). Tamano Bay, Japan. Living adult specimen on its food plant, *Caulerpa okamurai*. (Photo by Dr. Siro Kawaguti, reproduced by permission.)
- (Lower figure) *Berthelinia (Edenttellina) chloris belvederica* Keen & Smith, new subspecies. Holotype, CAS Paleo. Type Coll. No. 12317, Puerto Ballandra Bay, near La Paz, Baja California. Length, 8.5; height, 5.8 mm.



